Vocal evidence for restitution of species rank to a Santa Marta endemic: *Automolus rufipectus* Bangs (Furnariidae), with comments on its generic affinities

by Niels Krabbe

Some passerines in the family Tyrannidae possess entirely innate songs (Stein 1963, Lanyon 1978, Kroodsma 1984, 1989, Kroodsma & Konishi 1991), with no local dialects. A similar lack of dialects in several other families strongly suggests that song is innate in near-ly all suboscines, which has led to a recent re-evaluation of the taxonomic ranks of many forms (see, e.g., Remsen 2005). Several of these are members of the Furnariidae (Vaurie & Schwartz 1972, Whitney & Pacheco 1994, Kratter & Parker 1997, Zimmer 1997, 2002, Robbins & Zimmer 2005, Zimmer *et al.* 2008), which includes a large number of taxa that occur in dense and dark habitats, where vocalisations, rather than visual signals, probably play a major role in species recognition. The furnariid taxa *Furnarius cinnamomeus*, *F. lon-girostris*, *Synallaxis maranonica* and *Hyloctistes virgatus* are afforded species rank on the basis of vocal characters by some authors, whereas others (e.g. Remsen *et al.* 2007) await the pub-lication of vocal studies before accepting taxonomic changes.

During field work to document the voices of birds in the Sierra Nevada de Santa Marta, northern Colombia, in February 2007, I ascertained that the songs of several endemic taxa presently treated as subspecies are quite distinct from purported conspecifics. The present paper addresses *Automolus rubiginosus rufipectus*, described as a full species, Ruddy Foliage-gleaner *A. rufipectus*, by Bangs (1898), which differs so much from its alleged conspecifics that even its generic placement may demand re-evaluation. *A. rufipectus* was ranked as a subspecies of *A. rubiginosus* by Hellmayr (*in* Cory & Hellmayr 1925), a treatment that has been widely followed until the present.

Methods

I tape-recorded songs of four individuals of *rufipectus* at 1,200–1,800 m in the recently established ProAves Colombia reserve 'El Dorado' on the San Lorenzo ridge in the north-western part of the Sierra Nevada de Santa Marta, dpto. Magdalena, Colombia (11°06–08′N, 74°03–06′W). Birds were first taped under natural conditions and then attracted using play-back for identification. Three of the four recorded birds were seen, and one was photographed (Fig. 1) near its nest. Eight months later, an individual was collected near this nest (C. D. Cadena, specimen in Universidad de Los Andes, Bogotá, catalogue number ANDES-O-0433). Recordings were made using a Sennheisser ME67 microphone and a Sony TCM5000 tape recorder with Type I cassettes. Two additional recordings of *rufipectus* were consulted (Boesman 1999, Strewe *et al.* 2003).

Sonograms were compared among *rufipectus* and all other species or vocally distinct subspecies or subspecies-groups of *Automolus*, *Hylocryptus*, *Anabazenops* and *Syndactyla*, the latter three genera all encompassing species formerly included in *Automolus*. Sonograms were generated using the sound-editing program CoolEdit Pro (Syntrillium Software), which was also used for vocalisation analysis.

Observations on habitat and behaviour were noted in the field and are compared with published information.

Results

Vocalisations.—A total of 196 song phrases (from 5–6 different individuals) of *rufipectus* were analysed. Songs consisted of resonant notes (3–4 harmonics), given in a series of 4–6 similar notes, loudest at 1,800–3,000 Hz (second or third harmonic). Individual notes were up–downstrokes, the downstroke slightly more pronounced, and the peak volume at highest pitch. The loudest pitch was the second harmonic (1,800–2,000 Hz) in two or three individuals, the third harmonic (2,400–3,000 Hz) in two individuals, and second and third equally loud in one individual. The song was usually given in sets of two (less commonly one, rarely three) phrases, with a brief pause of 0.3–0.5 seconds between the two phrases. The first of the two phrases frequently had an extra, often slightly weaker and lower pitched introductory note, and was thus longer (0.42 ± 0.04 seconds) than the second (0.36 ± 0.03 seconds). The double phrases were delivered fairly regularly with pauses between them 2–4 seconds long.

All the individuals of *rufipectus* compared had similar songs, differing in virtually all aspects from songs of other forms of *Automolus rubiginosus* (Figs. 2a–i, 3a–b), the only similarities being the length of the song phrases and the tendency of *rufipectus* to deliver two song phrases in succession, a tendency also noticed in some individuals of other forms of *A. rubiginosus* from both Central America (*rubiginosus*, *veraepacis*, *saturatus*) and the Amazon (unnamed taxon). The song of *rufipectus* was more similar, indeed remarkably so, to the song of *Hylocryptus erythrocephalus* (Fig. 3b–c).

Calls of *rufipectus* recorded were churrs, two- to three-noted whilst foraging (Fig. 4d) and three- to four-noted when given in alarm (Fig. 4e), at 0.8–2.0 kHz (first and second, or second and third harmonic), lower pitched than song and differing distinctly from calls of both *A. rubiginosus* (Fig. 4a–b) and *Hylocryptus erythrocephalus* (Fig. 4c), which in turn have fairly similar calls except for the latter being lower pitched. No call resembling the high-pitched (4 kHz) call (not shown) purportedly given by *H. erythrocephalus* (Coopmans *et al.* 2004, cut 5; misidentified?) was ever heard from *rufipectus*.

Figure 1. *Automolus rufipectus*, Sierra Nevada de Santa Marta, Colombia, February 2007 (Joe Tobias)

Songs of eight of the other 13 currently recognised subspecies of *A. rubiginosus* (Remsen 2003), as well as of an unnamed taxon from the Amazonian lowlands, were compared (Fig. 2a–i). They all consist of a single, 0.3–0.6 seconds-long, distinctly rising note, sometimes (with intra-individual variation) possessing a short introductory note. As in other species of *Automolus*, the notes are highly resonant (with 3–4 audible harmonics), and as in *rufipectus* the pitch is variable. The single recording of the unnamed taxon from the Amazonian low- lands (all other forms being lower montane) is decidedly higher pitched (Fig. 2i), thus suggesting an isolated position of this form. The five forms for which no recordings were avilable at the time of the study were *guerrensis*, *fumosus*, *cinnamomeigula*, *venezuelanus* and *caquetae*. Songs of the former four are described as being similar to songs of adjacent forms (Howell & Webb 1995, Stiles & Skutch 1989, Hilty 2003; A. M. Cuervo pers. comm.). Only *caquetae* appears to be vocally unknown, but its poor morphological differentiation from, and seemingly continuous distribution with *brunnescens* suggest that it may be also similar.

Natural history.—On three occasions *rufipectus* was observed foraging. It remained within 0.5 m of the ground, and spent most of its foraging time on the ground, rummaging among large dead leaves as does *Hylocryptus erythrocephalus* (Ridgely & Greenfield 2001, Remsen 2003; pers. obs.), only once pecking briefly at a decaying trunk as does *Automolus rubiginosus* regularly (Remsen 2003; J. A. Tobias pers. comm.). This concurs with Todd & Carriker (1922), who wrote that it 'does little climbing, but keeps hopping about on or near the ground'. A vertical bank with several entry holes 1–2 m above was found. The bird would always leave from the same hole when disturbed, but when entering, it would usually briefly enter one of the other holes before moving to the final one.

Habitat.—*A. rufipectus* was found in forest and second-growth habitats, which were transitional between the dry *Acacia* scrub at sea level and the humid forest above 2,100 m, but more similar to the latter. The undergrowth was dense, and the litter included many large leaves. In February, a dry month with occasional rain, the habitat at 1,200–1,800 m was reminiscent of dry-forest haunts of *Hylocryptus erythrocephalus* in south-west Ecuador and north-west Peru. On two occasions I found *rufipectus* in heavily disturbed areas. Todd & Carriker (1922) noted: 'It is partial to the heavy forest or thick second growth, and is fond of dark tangles and ravines'. I did not find it or its habitat above 1,800 m on the San Lorenzo ridge 70 km east-north-east of Pueblo Viejo (the type locality). This is evidently in agreement with Carriker's experience; although the type of *rufipectus* was originally said to have been taken at *c*.8,000 feet [2,438 m] (Bangs 1898), Todd & Carriker (1922) gave the species' altitudinal range as 3,000–6,000 feet [914–1,829 m], and added the note '7500 feet, according to Mr Brown' [the collector of the type]. The nest I found on the San Lorenzo ridge was at *c*.1,750 m.

Distribution, population and conservation.—All records are from the north-western and northern slopes of the Santa Marta Mountains. Collecting sites are from around the San Lorenzo ridge (Cincinnati; Las Vegas; Agua Dulce) and in the upper río Ancha drainage (La Concepción; San Antonio; Pueblo Viejo; Chirua; Heights of Chirua) in dptos. Magdalena and Guajira (Todd & Carriker 1922). These and some additional, more recent sight or vocal records were mapped by R. Strewe, G. Lobaton & S. Sanchez, of Fundación ProSierra Nevada, in 2004 (see http://www.alpec.org/Atlas/Tama%F1oFinal/Automolus rubiginosus.jpg). However, the southern slopes of the mountains (large parts of which have been converted for coffee farming) have been subject to very little ornithological investigation to date. I found the species widespread but uncommon on the San Lorenzo
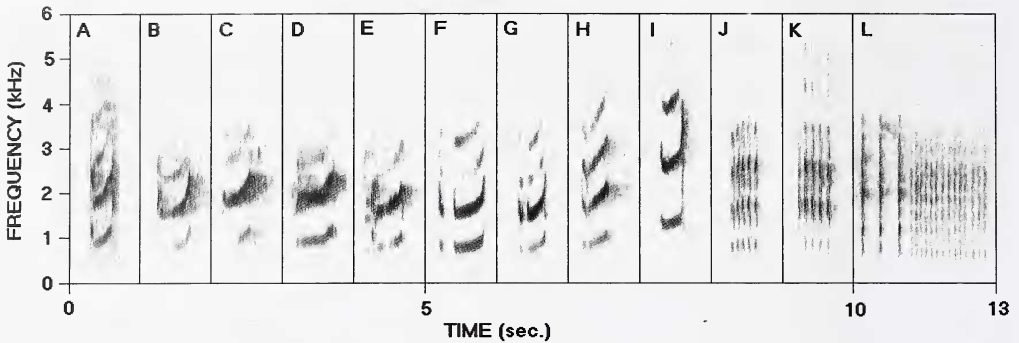
Figure 2. Songs of 12 taxa of foliage-gleaners. A–J ten different subspecies of *Automolus rubiginosus*: A: *rubiginosus* (Oaxaca, Mexico; P. Boesman). B: *veraepacis* (Chiapas, Mexico; P. Boesman). C: *saturatus* (Darien, Panama; L. R. Macaulay). D: *nigricauda* (Pichincha, Ecuador; N. Athanas). E: *sasaimae* (Boyacá, Colombia; O. Laverde). F: *obscurus* (Surinam; O. Ottema). G: *brunnescens* (Zamora-Chinchipe, Ecuador; N. Krabbe). H: *watkinsi* (Pando, Bolivia; T. S. Schulenberg). I: possibly the unnamed taxon referred to by Remsen (2003) (Amazonas, Brazil; C. A. Marantz). J: *rufipectus* (Magdalena, Colombia; N. Krabbe). K: *Hylocryptus erythrocephalus* (Loja, Ecuador; N. Krabbe). L: *Hylocryptus rectirostris* (Minais Gerais, Brazil; H. G. Remold).
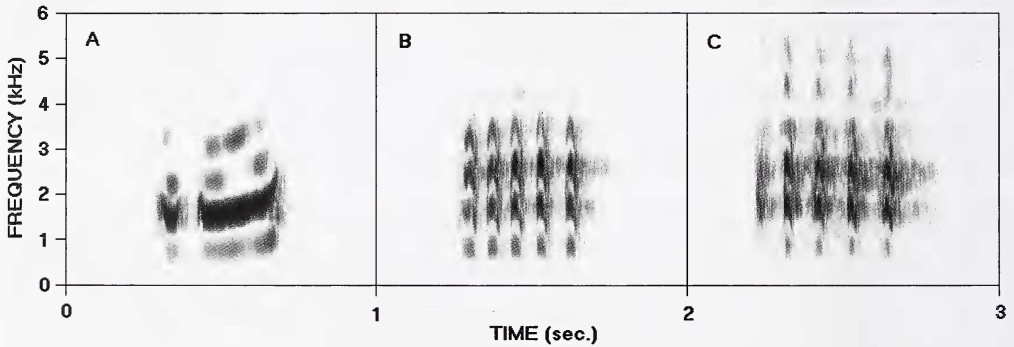

Figure 3. Songs of three foliage-gleaners. A: *Automolus rubiginosus brunnescens*. B: *A. r. rufipectus*. C: *Hylocryptus erythrocephalus*. Same as Fig. 2G, J and K, but with a different time scale.
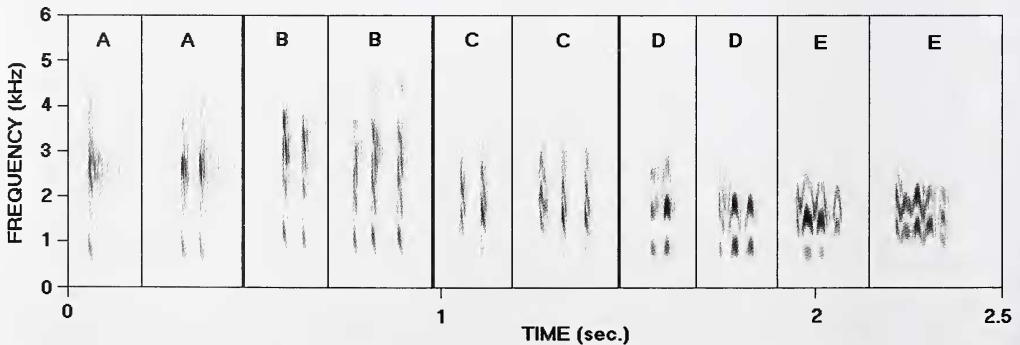

Figure 4. Calls of four taxa of foliage-gleaners. A: *Automolus rubiginosus brunnescens* (Napo, Ecuador; N. Krabbe). B: *A. r. nigricauda* (Esmeraldas, Ecuador; O. Jahn). C: *Hylocryptus erythrocephalus* (Piura, Peru; H. van Oosten). D–E: *Automolus rubiginosus rufipectus* (Magdalena, Colombia; N. Krabbe), D foraging calls, E alarm-calls. Note time scale.

ridge, apparently occurring wherever there was available habitat. The two closest territories found were *c*.200 m apart. Todd & Carriker (1922) noted 'It was perhaps most numerous at Pueblo Viejo in the thick scrub, but cannot be considered a common bird anywhere'. Large

areas around Pueblo Viejo have been denuded by burning, but considerable expanses of forest and scrub occur between Pueblo Viejo and the San Lorenzo ridge. In view of the species' tolerance of disturbed habitats, there seems to be no grounds for considering it immediately threatened. It is probably best given the IUCN status of Near Threatened, approaching the status of Vulnerable (criteria B1(b), B2(b) and C1). To my knowledge, only a small part of its range is effectively protected (the 'El Dorado' reserve on the San Lorenzo ridge). The Sierra Nevada de Santa Marta National Park only includes higher elevations in this part of the mountains, and nearby Tayrona National Park only elevations below the range of *rufipectus*.

Discussion

A detailed study and analysis may reveal the small differences between songs of some of the other subspecies of *Automolus rubiginosus* to be constant and perhaps sufficiently different for species recognition (see Remsen 2003), were they ever to come into contact. However, their close similarity to each other suggests that they likely form a monophyletic unit. In contrast, lesser vocal differences between *A. rufipectus* and *H. erythrocephalus* suggest that *A. rufipectus* may not be a close relative of its proposed congeners and conspecifics. The habitat of *rufipectus* is distinctly drier than those of other forms referred to *A. rubiginosus*. However, in absence of a study of molecular or other characters, convergent evolution cannot be ruled out.

Independent of whether *rufipectus* is a close or distant relative of other taxa currently placed in *A. rubiginosus*, the dramatic vocal differences demonstrate that *rufipectus* merits species recognition. The two sympatric species *A. infuscatus* and *rufipileatus* differ in fewer vocal variables (Fig. 5a–c), indicating that even small vocal differences may be sufficient for species recognition in foliage-gleaners. I therefore recommend that species rank be restituted for *rufipectus*. Santa Marta Foliage-gleaner (rather than Rufous-chested Automolus as employed by Cory & Hellmayr 1925) might be an appropriate vernacular name.

Vocalisations of the other six species referred to *Automolus* (Figs. 5a–g, 6a–c, 7a) are highly diverse and do not, in general, offer clues as to relationships among species. Only songs of *infuscatus* and *rufipileatus* (Fig. 5a–c) bear sufficient resemblance to each other that they could be confused by experienced field ornithologists.

Inter-relationships among the ten presently recognised genera of foliage-gleaners and allies are unclear, and several genera are so poorly defined that the the only solution to avoid problems in defining them morphologically would be to merge them all (Remsen 2003). In relation to other furnariids, the multiple-gene molecular studies by Irestedt *et al.* (2006; unpubl. data) provide strong evidence that foliage-gleaners and allies (including *Megaxenops* and *Heliobletus*) form a monophyletic unit; within the foliage-gleaner assembly these authors found two clades, one comprising *Automolus*/*Hyloctistes*, *Hylocryptus*/*Clibanornis* and *Thripadectes*, and the other consisting of *Philydor*, *Syndactyla*, *Anabacerthia*, *Heliobletus* and *Megaxenops*.

Genus *Hylocryptus* was erected for *erythrocephalus* when that species was described by Chapman (1919), mainly on the basis of its long, straight bill. Hellmayr (*in* Cory & Hellmayr 1925) left *rectirostris* in *Automolus*, but noted that its juvenile plumage and certain structural characters suggest affinities with *erythrocephalus*. Despite the widely disjunct distributions of the two species, Zimmer (1936) had 'no hesitation' in assigning *rectirostris* to *Hylocryptus*, partly because of its similar general colour pattern to *erythrocephalus*, but primarily because its bill, though shorter, approaches that of *erythrocephalus* in length and shape. Zimmer's treatment has been followed by all subsequent authors. Songs of the two
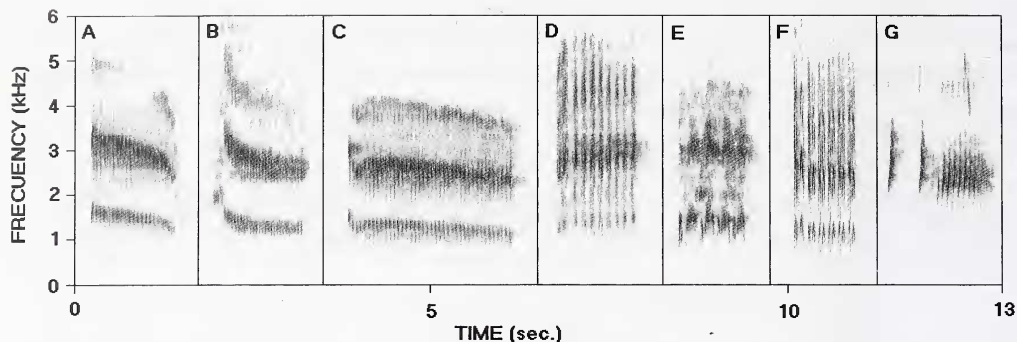
Figure 5. Songs of different *Automolus* foliage-gleaners. A: *A. rufipileatus consobrinus* (Sucumbíos, Ecuador; J. V. Moore). B: *A. infuscatus badius* (Amazonas, Venezuela; C. Parrish). C: *A. i. turdinus* (Orellana, Ecuador; R. S. Ridgely). D: *A. paraensis* (Mato Grosso, Brazil; C. A. Marantz). E: *A. leucophthalmus lammi* (Alagoas, Brazil; C. A. Marantz). F: *A. l. sulphurascens* (Rio de Janeiro, Brazil; L. P. Gonzaga). G: *A. melanopezus* (Orellana, Ecuador; R. S. Ridgely).
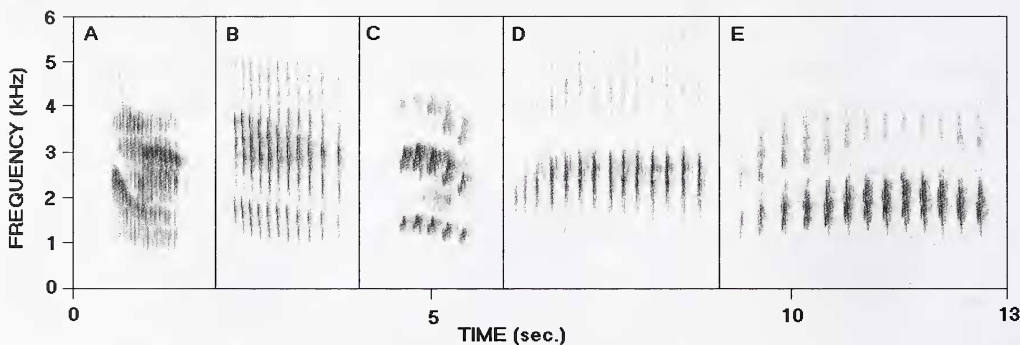

Figure 6. Songs of different *Automolus* and *Anabazenops* foliage-gleaners. A: *Automolus ochrolaemus cervinigularis* (Veracruz, Mexico; L. Irby Davis). B: *Automolus o. exsertus* (Costa Rica; L. Irby Davis). C: *Automolus o. turdinus* (Sucumbíos, Ecuador; P. Coopmans). D: *Anabazenops fuscus* (Rio de Janeiro, Brazil; T. A. Parker). E: *Anabazenops dorsalis* (Mato Grosso, Brazil; M. D. Medler).
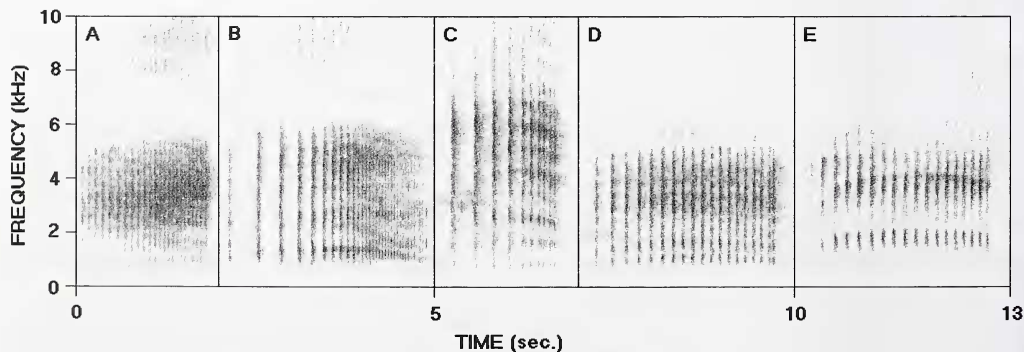

Figure 7. Songs of different *Automolus* and *Syndactyla* foliage-gleaners. A: *A. r. roraimae* (Bolívar, Venezuela; M. Van Beirs) (species removed to *Syndactyla* by Zimmer *et al.* 2008). B: *S. ruficollis* (Loja, Ecuador; N. Krabbe). C: *S. subalaris mentalis* (Napo, Ecuador; M. Lysinger). D: *S. g. guttulatus* (Aragua, Venezuela; C. A. Marantz). E: *S. rufosuperciliata cabanisi* (Zamora-Chinchipe, Ecuador; N. Krabbe). For sonograms of *S. dimidiata* see Robbins & Zimmer (2005). Note frequency scale.

species have rather different patterns, but show some similarity in pitch and quality (Fig. 2k–l).

The resemblance of the song of *rufipectus* to that of the much longer and straighter billed *Hylocryptus erythrocephalus* (Figs. 2j–k, 3b–c) might be coincidental, as perhaps also suggested by their different calls (Fig. 4c–e), but is so striking, that the possibility that they are sister taxa demands consideration. Were such a relationship confirmed, it would add to the already interesting evolutionary and biogeographic history of the genus *Hylocryptus* (which would comprise three relictual species with disjunct distributions in widely separated dry-forest areas of the Neotropics). It would also show that songs of foliage-gleaners, even in relatively small populations, may remain unchanged for extended periods of time, and would call for additional caution when using bill shape as a taxonomic character in this group. A similar case of vocal resemblance in song between forms whose morphologies do not suggest that they are closely related has been reported between the fairly straight-mandibled (and rather uniform) *Automolus roraimae* (Fig. 7a) and the distinctly recurve-mandibled (and more or less streaked) members of the genus *Syndactyla* (Fig. 7b–e) (see also Hilty 2003, Robbins & Zimmer 2005, Zimmer *et al.* 2008). In view of the highly disputed merging of many foliage-gleaner genera by Vaurie (1980) (see Remsen 2003, Robbins & Zimmer 2005) and the conflicting indications of morphological and vocal data as to the relations of the taxon *rufipectus*, I would propose awaiting the results of a molecular study before making a generic change for this foliage-gleaner.

The Sierra Nevada de Santa Marta is an isolated massif in northern Colombia with an area of *c*.5,900 km². With no fewer than 70 endemic bird taxa, it is perhaps the most diverse smaller centre of terrestrial endemism in the world. Most of the endemic taxa are derived from Andean forms (Todd & Carriker 1922), and their many different levels of differentiation suggest that multiple colonisations have occurred. Seventeen are presently ranked as species by Remsen *et al.* (2007). Many of these species are in groups with colourful plumage, whilst many suboscines remain ranked only as subspecies. It therefore comes as no great surprise that *A. rufipectus* is better ranked as a biological species. Preliminary analyses of vocalisations suggest that species rank is likely to be appropriate for several other taxa endemic to the Santa Marta mountains, such as *Trogon personatus sanctaemartae*, *Lepidocolaptes lacrymiger sanctaemartae*, *Grallaria rufula spatiator*, *Henicorhina leucophrys anachoreta*, *Arremon torquatus basilicus* (already shown to be genetically distinct by Cadena 2006, Cadena *et al.* 2007), and possibly others.

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APPENDIX

Songs examined. Abbreviations used are: XC = Xeno-canto website at www.xeno-canto.org; LNS = Macaulay Library of Natural Sounds, Cornell, website at www.animalbehaviorarchive.org/loginPublic.do. Recordings known to be given by an individual already represented, were avoided or counted as one.

Automolus rubiginosus: *A. r. rubiginosus* 6 (Boesman 2007; LNS 89684, 95077, 127210, 127230, 127246, 127247, 127271); *A. r. veraepacis* 3 (Boesman 2007; XC 11012, 14140); *A. r. saturatus* 1 (LNS 108866); *A. r. nigricauda* 9 (Jahn *et al*. 2002, Krabbe & Nilsson 2003; XC 5576, 6598, 8000, 8308 (call), 13139); *A. r. sasaimae* 1 (XC 12728, 12729, 12731); *A. r. obscurus* 1 (XC 7520); *A. r. brunnescens* 4 (Krabbe & Nilsson 2003; XC 6575; also an unpubl. recording of calls by N. Krabbe); *A. r. watkinsi* 1 (Schulenberg *et al*. 2000); *A. r.* ssp. nov.: 1 (LNS 117196, 117197).

Automolus rufipectus: 6 (Boesman 1999; Strewe *et al*. 2003; also songs of four individuals and calls of one recorded during the present study).

Automolus roraimae: 3 (Boesman 2007).

Automolus ochrolaemus: *A. o. cervinigularis* 5 (LNS 7009, 7011, 7012, 102599; XC 14133); *A. o. hypophaeus* 2 (LNS 7012; XC 11011); *A. o. exsertus* 1 (LNS 7013); *A. o. pallidigularis* 11 (Jahn *et al*. 2002, Krabbe & Nilsson 2003; LNS 7014, 82449; XC 1490, 12898); *A. o. turdinus* 12 (Krabbe & Nilsson 2003, Moore 1993; XC 6094, 8704; also 7 unpubl. recordings from Ecuador by P. Coopmans and J. V. Moore); *A. o. ochrolaemus* 5 (LNS 39003; XC 85, 8361, 8538, 13424); *A. o. auricularis* 4 (LNS 88948; XC 9540, 9541, 14773).

Automolus infuscatus: *A. i. infuscatus* 15 (Boesman 2007, Krabbe & Nilsson 2003, Moore 1993; XC 3434, 10324; LNS 53363, 53377, 110437; also 4 unpubl. recordings from Ecuador by P. Coopmans, M. Lysinger, J. V. Moore and R. S. Ridgely); *A. i. badius* 4 (Boesman 2007; LNS 117037; XC 6229).

Automolus paraensis (see Zimmer 2002): 11 (LNS 88849, 88900, 88950, 89066, 89067, 106198, 110005, 113065, 115019, 115233, 115237).

Automolus leucophthalmus: *A. l. lammi* 3 (LNS 127914, 127950, 127992); *A. l. sulphurascens* 10 (Gonzaga & Castiglioni 2001; LNS 19082, 19086, 19214, 113312, 113394, 113395, 115354, 115426, 115429).

Automolus rufipileatus: *A. r. consobrinus* 22 (Krabbe & Nilsson 2003, Moore 1996; LNS 115874, 119700, 110635, 106422, 110523, 129499, 129534; XC 222, 3206, 6409, 9926, 13425; also 4 unpubl. recordings from Ecuador by J. V. Moore and R. S. Ridgely); *A. r. rufipileatus* 8 (LNS 88386, 88462, 88522, 88634, 88668, 106104, 10630, 109948).

Automolus melanopezus: 13 (Krabbe & Nilsson 2003; LNS 26565, 38862, 38865, 38885, 38914; XC 12027; Moore 1993; also 5 unpubl. recordings from Ecuador by P. Coopmans, M. Lysinger, J. V. Moore and R. S. Ridgely).

Hylocryptus erythrocephalus: 11 (Coopmans *et al*. 2004, Krabbe & Nilsson 2003; LNS 122729; XC 4152, 4191, 8306, 8308 (call), 8727, 14414).

Hylocryptus rectirostris: 2 (LNS 114856; XC 11924).

Anabazenops fuscus: 8 (Gonzaga & Castiglioni 2001; LNS 39082, 103868, 112723; XC 4861, 4862, 5468, 14680).

Anabazenops dorsalis: 8 (LNS 88418, 106182, 106092, 106175, 106200, 109946; XC 6574, 11902).

Syndactyla guttulata: *S. g. guttulata* 6 (Boesman 2007; LNS 127816, 127819).

Syndactyla ruficollis: 6 (Coopmans *et al*. 2004, Krabbe & Nilsson 2003).

Syndactyla rufosuperciliata: *S. r. rufosuperciliata* 2 (Gonzaga & Castiglioni 2001; LNS 108238); *S. r. acrita* 2 (LNS 19094; XC 8195); *S. r. oleaginea* 1 (Krabbe *et al*. 2001); *S. r. cabanisi* 3 (Lysinger *et al*. 2005, Krabbe & Nilsson 2003).

Syndactyla subalaris: *S. s. mentalis* 3 (Moore & Lysinger 1997, Krabbe & Nilsson 2003); *S. s. subalaris* 3 (Krabbe & Nilsson 2003).